

Testing the "Ecologically Noble Savage" Hypothesis: Interspecific Prey Choice by Piro Hunters of Amazonian Peru¹

Michael S. Alvard²

Native peoples have often been portrayed as natural conservationists, living in "harmony" with their environment. It is argued that this perspective is a result of an imprecise definition of conservation that emphasizes effects rather than actual behavior. Using foraging theory as a contrast, an operational definition of conservation is offered. Foraging theory assumes that foragers will behave to maximize their short-term harvesting rate. Hunting decisions that are costly in terms of short-term harvest rate maximization, yet increase the sustainability of the harvest are deemed conservation. Using this definition, alternative hypotheses are tested using data on the inter-specific prey choice decisions of a group of subsistence hunters, the Piro of Amazonian Peru. Results indicate that hunters do not show any restraint from harvesting species identified as vulnerable to over-hunting and local extinction. Decisions are made that are consistent with predictions of foraging theory.

KEY WORDS: hunting; conservation; foraging theory; Amazonia; Peru.

INTRODUCTION

With the threat to the world's environment becoming more apparent, quick and politically expedient solutions have increasingly been sought from indigenous peoples. In contrast to modern industrialized societies, it has been argued that native peoples constitute the last vestiges of a wise and balanced existence with nature. Jean Jacques Rousseau's concept of the

¹The phrase "ecologically noble savage" was coined by Kent Redford (1991) in a thought provoking article of the same name.

²Department of Anthropology, Dickinson College, Carlisle, Pennsylvania 17013.

"Noble Savage" has been extended and re-defined into the "Ecological Noble Savage" by both conservationists and anthropologists (Redford, 1991). Such "primitive" human economies are thought by many to maintain a type of harmony with their environments by developing cultural institutions and customs that function to conserve the animals and plants the people rely on for food (Speck, 1939; Meggers, 1971; Bodley, 1976, 1990; McDonald, 1977; Clay, 1988; see Alvard, 1993 for other citations). The idea that industrialized peoples can learn from native peoples how to live "in balance" with nature is common (Posey, 1985; Bunyard, 1989).

There is no doubt that indigenous people have an intimate knowledge of their environment, perhaps rivaling Western scientific specialists in some areas (Berlin and Berlin, 1977). A number of researchers have recently questioned, however, the view of native peoples as benign stewards of nature (Diamond, 1986; Hames, 1987, 1991, Redford, 1991; Kay, 1990; Simms, 1992; Heinen and Low, 1992; Alvard, 1993). As noted by Hames (1987), it remains to be proven whether native knowledge is utilized to maintain a balance with nature, or simply to procure resources in the most efficient manner possible. This point needs to be stressed: while there is ample evidence that native peoples have a truly deep and intimate knowledge of their environment, it does not necessarily follow, and has not been empirically demonstrated, that they use this knowledge to maintain any sort of equilibrium with their environment or to conserve the resources they use.

I have argued elsewhere (Alvard, 1993, 1994), that many of the misconceptions concerning the apparent conservation proclivities of traditional peoples are a result of an imprecise understanding of what constitutes conservation. Conservation cannot be simply identified by effects. That is, observing a native group in equilibrium with its environment is not sufficient evidence to label them conservationists. Sustainable harvests can be easily maintained by small groups of consumers living in an abundant environment. In such situations, hunters could be exceedingly wasteful yet not have a large enough impact to cause a significant negative impact on their prey. Hunn (1982) refers to apparent conservation in such contexts as epiphenomenal conservation. To avoid identifying epiphenomenal conservation as genuine conservation, a nonambiguous definition is required. Such a definition has been developed from a context of foraging theory. How foraging theory contributes to an operational definition of conservation is reviewed below.

CONSERVATION AND FORAGING THEORY

Besides the empirical shortcomings of the conservationist arguments, there is little theoretical justification for expecting individuals to conserve

open access resources like those usually exploited by subsistence peoples (Alvard, 1993). Open access resources are those that all consumers can harvest without restriction (McCay and Acheson, 1987). Economic theory argues open access resources are subject to the "tragedy of the commons," where economically rational individuals do better by exploiting resources, even as those resources are driven to ruin (Hardin, 1968). In a related argument, evolutionary theory points out it is very difficult for natural selection to produce behavioral traits that compel individuals to behave in ways beneficial to the group if those behaviors are contrary to their own best interests (Williams, 1966). Group selection, which was originally argued to evolve in individuals with traits that regulate and restrain their reproduction to prevent the overexploitation of resources (Wynne-Edwards, 1962), has been found to be important in only limited numbers of contexts (Lewontin, 1970).

According to the theory of evolution, natural selection favors traits that maximize the reproductive success of individuals that possess them. Since a large component of any organism's reproductive success depends on how well it can acquire resources, it is expected that food acquisition behavior is under strong optimizing selection. Foraging theory is a branch of evolutionary theory that has been used to examine subsistence behavior and feeding across a wide variety of taxa including humans (Stephens and Krebs, 1986). More food is assumed to increase fertility and survivorship, while minimizing the amount of time spent foraging allows the forager to engage in other fitness enhancing activities (Kaplan and Hill, 1992). Foragers hunting according to the assumptions of foraging theory are expected to maximize their short-term harvesting rate (i.e., the rate at which resources are harvested per unit time). I will refer to such foragers as rate-maximizers. Individuals that are truly altruistic, and restrain from taking more of a resource than would be in their best interest for reasons of conservation, are expected to be replaced through natural selection by more selfish and exploitive actors.

Conservation-as-altruism should not be confused with conservation-as-selfishness, however. The problems with group selection suggest that individuals are unlikely to pay a cost and conserve resources for the benefits of the larger society. It is conceivable, however, that conservation could evolve as a selfish strategy if the short-term cost allows a high enough long-term payoff to the individual actor. The evolution of a conservation strategy is an interesting problem that involves issues of discounting and time preference (Rogers, 1991; see also Alvard, 1994). This paper does not address the question of how conservation might evolve, but rather is directed at using an operational definition of conservation to test for its presence among a group of neotropical hunters.

Foraging models are used in this paper to generate alternative predictions to conservation, not because evolutionary theory rules out conservation as a strategy *per se*, but rather because simple foraging models make assumptions of short-term return maximization which contrast with the goals of conservation. Foraging theory also provides an excellent context for conservation behavior to be defined more explicitly so that the problems of confusing epiphenomenal conservation with genuine conservation, mentioned above, can be avoided.

Definition of Conservation

Conservation behavior has tended to be identified by looking for effects rather than by examining the decisions of individuals. This is problematic because a small band of hunters, whether maximizing their return rates, or hunting in a grossly wasteful way, could be hunting sustainably depending on the nature of the resources targeted. Such "conservation" is epiphenomenal, as described above (Hunn, 1982).

Since rate-maximizing foragers can hunt in a sustainable manner depending on the context, conservation needs to be defined in terms beyond those of sustainable harvesting. Inherent in the concept of conservation is the notion of restraint. Conservation can be thought of as enduring a cost in the present so that some benefit will be realized in the future (see Rogers, 1991). This idea is contrary to the assumptions of foraging theory, which argues that hunters will do whatever is required, given constraints, to maximize returns in the short-term. If there is no restraint from what is optimal in the short-term for the actor, the behavior in question cannot be discerned from the basic predictions of foraging theory (see Alvard, 1993, 1994). Conservation, then, can be operationally defined in contrast to short-term rate maximizing. Hunting decisions that are costly in terms of short-term harvest rate maximization, yet increase the sustainability of the harvest are deemed conservation (see Alvard, 1993, 1994). This definition solves the problem inherent in using effects, such as sustained harvest, as evidence for conservation and allows for more robust hypotheses testing.

THE TWO HYPOTHESES

This paper is the first in a series that tests predictions generated from two alternative hypotheses regarding subsistence hunters and conservation of their prey. The first hypothesis states that native peoples are conserva-

tionists. It argues that hunting decisions are made to ensure sustainable harvests of prey. Restraint is exercised by hunters in the short term to prevent overexploitation and depletion of resources in the long term. The second hypothesis, derived from foraging theory, argues that hunters will overexploit resources whenever it is to their advantage to do so. This hypothesis assumes that short-term harvest rate maximization, not long-term conservation, guides hunters' behaviors. (Stephens and Krebs, 1986).

The data presented below address predictions regarding interspecific prey choice by a group neotropical subsistence hunters, the Piro. Future papers will test predictions concerning intra-specific prey choice, patch choice, depletion, and harvest sustainability (see Alvard, 1993). The broad questions of importance here are: Since, as I will show, the prey available to hunters vary in regard to vulnerability to overexploitation and local extinction, do their interspecific prey choices represent a conservation oriented decision? Or, do hunters choose prey that are optimal in terms of return rate maximization? Evidence for conservation would consist of hunters forgoing opportunities to kill vulnerable species that are nonetheless predicted by foraging theory to be pursued.

The paper will proceed as follows. I will first introduce the study group, study site, and the important prey species. Then, I will briefly review the methods used to identify prey choice decisions. Following this, I will outline the predictions of each hypothesis and test them using data from the study population. I will conclude with a discussion of the results.

THE PIRO

The data presented in this paper were collected from the Arawakan speaking Piro community of Diamante, situated in the lowland rain forest environment of southeastern Peru. The village is located on the Alto Madre de Dios River on the southeast border of Manu National Park, approximately 175 km northeast of the town of Cuzco (see Fig. 1).

The Piro are hunter-fisher-farmers. Cultivation of manioc and plantains supply the bulk (71%) of the calories consumed. Hunting and fishing with a variety of technologies provide 14% of the calories and most of the protein and fat in their diet. The remaining 15% of the calories are from forest products, domestic fruits, and commercial foods (Alvard, 1993).

The Piro have had a longer recent history of contact with the Peruvian culture than have their neighbors the Machiguenga, another group who live inside the park. Both groups, however, have had intermittent contact with the Inca, Spanish, rubber workers, colonists, various missionary groups, and anthropologists over the 500 years (Camino, 1977; Alvard, 1993). The

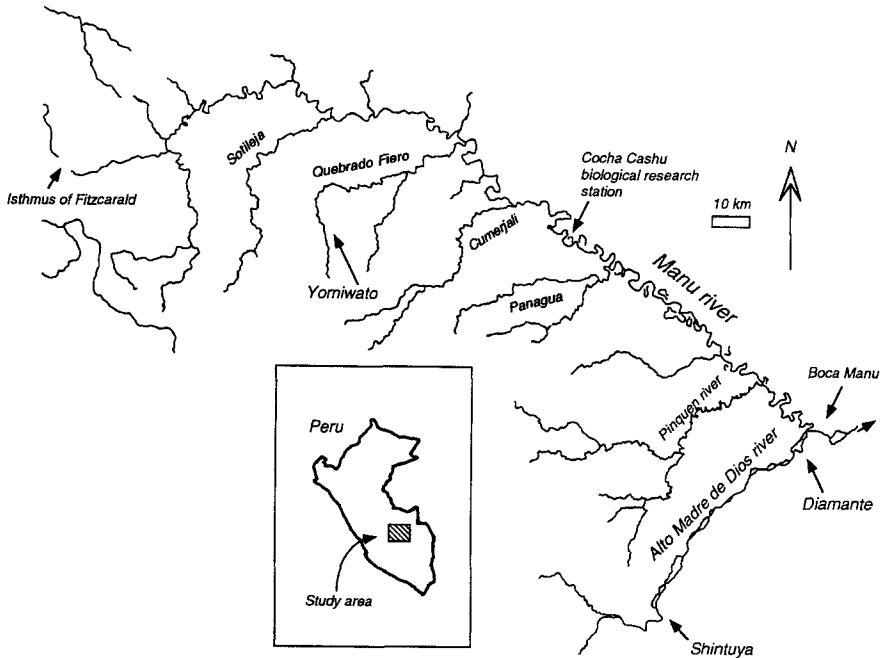


Fig. 1. Map of the Manu region. Manu National Park encompasses the entirety of the Manu River watershed. The Alto Madre de Dios River is the Southeastern border of the park. Diamante is located near the confluence of the two rivers.

inhabitants of Diamante are not restricted in their economic development as are the natives living inside Manu Park. As a result, the Piro have more access to nontraditional technologies.

Germane to this study is the technology employed by hunters. While bows were commonly used, 85% of the meat (by weight) acquired from hunting was procured with shotguns. Seven shotguns were present in the village at the time of the study. The weapons are 16-gauge, single shot breechloaders. They were obtained over the course of the last 15 years, primarily from the local Catholic priest. The shells, containing lead shot, are also obtained from the priest but occasionally can be purchased or traded from river traders. As demonstrated with other Amazonian groups (Hames, 1979; Yost and Kelly, 1983), and at Diamante, Piro shotgun hunters are much more efficient than bow hunters (Alvard and Kaplan, 1991).

The present study benefits from the work conducted at the biological research station of Cocha Cashu. The station is located inside Manu Park National Park, on the Manu River approximately 90 km from the village of Diamante. John Terborgh and his students have been conducting eco-

Table I. Common and Scientific Names of Animals and Birds Encountered During Hunts at Diamante or Otherwise Mentioned in Text

Animal type	Common name	Scientific name
Ungulates	Brazilian tapir	<i>Tapirus terrestris</i>
	Red Brocket Deer	<i>Mazama americana</i>
	Gray brocket deer	<i>M. gouazoubira</i>
	Collared peccary	<i>Tayassu tajaca</i>
	White lipped peccary	<i>T. pecari</i>
Primates	Woolly monkey	<i>Lagothrix lagothricha</i>
	Spider monkey	<i>Ateles paniscus</i>
	Howler monkey	<i>Alouatta seniculus</i>
	Brown capuchin monkey	<i>Cebus apella</i>
	White capuchin monkey	<i>C. albifrons</i>
	Squirrel monkey	<i>Saimiri sciureus</i>
	Titi monkey	<i>Callicebus moloch</i>
	Black mantled tamarin	<i>Saguinus nigricollis</i>
Rodents	Night monkey	<i>Aotus</i> spp.
	Capybara	<i>Hydrochaeris hydrochaeris</i>
	Paca	<i>Agouti paca</i>
	Agouti	<i>Dasyprocta variegata</i>
Edentata	Squirrel	<i>Sciurus</i> sp.
	Giant armadillo	<i>Prionates maximus</i>
	Armadillo	<i>Dasypus novemcinctus</i>
	Collared anteater	<i>Tamandua tetradactyla</i>
Carnivores	Two-toed sloth	<i>Choloepus</i> sp.
	Jaguar	<i>Panthera onca</i>
	Puma	<i>Felis concolor</i>
	Ocelot	<i>F. pardalis</i>
	Tayra	<i>Eira barbara</i>
	Nutria	<i>Lutra longicaudis</i>
	Giant otter	<i>Pteronura brasiliensis</i>
	Coati	<i>Nasua nasua</i>
Birds (Cracids)	Short eared dog	<i>Atelacynus microtis</i>
	Spix's guan	<i>Penelope jacquacu</i>
	Guan	<i>Aburria pipile</i>
	Currassow	<i>Mitu mitu</i>
Birds (others)	Tinamous	<i>Crypturellus</i> spp.
	Tinamous	<i>Tinamus</i> spp.
	Macaws	<i>Ara</i> spp.
	Toucan	<i>Ramphastos</i> spp.
	Wood quail	<i>Odontophorus</i> spp.
	Trumpeter	<i>Psophia leucoptera</i>
	Harpy eagle	<i>Harpia harpyja</i>

logical studies at Cocha since the early 1970s. As a result, the area is one of the best scientifically known tropical regions of the world (Terborgh, 1983; Gentry, 1990). Although the study site at Diamante differs in some respects from the forest at Cocha Cashu, both forests are classified as moist tropical rain forest according to the Holdridge system (Holdridge, 1967), and enough similarities exist that a comparison is useful.

Terborgh, Fitzpatrick, and Emmons (1984) report 99 species of mammals, including 13 species of non-human primates, and 526 species of birds within the Park's boundaries. Only a relatively small number of these species are preyed upon by the Piro; fewer still are important in their diet either in terms of numbers killed or total biomass harvested. The species important in the diet of the Piro include ungulates: the Brazilian tapir (*Tapirus terrestris*), collared peccary (*Tayassu tajacu*), and red brocket deer (*Mazama americana*). Capybara (*Hydrochaeris hydrochaeris*), a large rodent, is taken frequently. Black spider (*Ateles paniscus*) and red howler monkeys (*Alouatta seniculus*) are the two important primates in the diet (see Alvard, 1993; Alvard and Kaplan, 1991 for more details on these species). Table I lists these and other species encountered during observed hunts with the Piro.

METHODS

Data were collected in Diamante during two field sessions. The first was accomplished from August 1988 through May of 1989; the second from October 1990 to May 1991. I employed both behavioral observation and interview methods to obtain the data presented below. A modified form of focal individual sampling (Altman, 1974; Borgerhoff-Mulder and Caro, 1985) was used to directly observe hunting behavior. Thirty hunts were observed in 1988–1989 for a total of 291.2 hunter/hours; 49 hunts were observed in 1990–1991 for 401.8 hunter/hours.

When a focal individual hunting day was scheduled, the adult men in the community were surveyed to determine who would be hunting (this was done either the night before or in the early morning) and a man who was amenable to being followed was chosen. While it would have been desirable to randomize the hunting sample with respect to the hunters in the village, this was not possible. Some hunters showed no interest in having an anthropologist accompany them; there also existed much variability in how often individual men hunted. Thus, while an attempt was made to observe most hunters at least once, the observed hunt sample is skewed toward hunters who hunted frequently and with whom I had a friendly relationship.

During focal follows hunters were followed into the forest and a number of their activities were recorded. The behaviors pertinent to this analysis include: travel, encounters with prey, pursuit, and kill. A detailed record of the location and time was also maintained. Encounters were defined by the hunter's report of his awareness of a potential prey animal or by his behavior. Pursuits were defined as any change in behavior from search to active attempts to chase or shoot the animal. Tracking prey was defined as search rather than pursuit. The following information was obtained for all animals killed: species, sex, age, reproductive status, weight, and technology used. Animals encountered but not pursued, or encountered and pursued but not killed were also identified as far as possible.

Besides these directly observed hunts, to increase the sample for which some information is known, and to provide a more random representation, interviews were conducted concerning hunts not directly observed. Interviews were designed to be simple, unambiguous and consisted of questions relating to the date, the participants, and the location of the hunt. Since the Piro were familiar with western time-keeping, and were remarkably good at assigning times by the location of the sun in the sky, times of departure and return were elicited as well. Hunters were asked to list all game encountered, those pursued and those killed. A total of 120 interviews were conducted.³ While the observed hunts were primarily shotgun hunts, the interview sample had many bow hunts. Shotguns were taken on 69 of the unobserved hunts (719.7 hunter/hours), while bows were the sole weapon for 51 of the hunts (606 hunter/hours).

THE TWO HYPOTHESES IN MORE DETAIL

Conservation

The ability of different prey to withstand various levels of harvest without depletion varies with the population dynamics of the species (Caughley, 1977). While every species is able to withstand some level of harvest, some are particularly susceptible to over exploitation and local extinction because of slow reproductive rates (Robinson and Ramirez, 1982, see below). If indigenous people possess an intimate knowledge of their environment, it is not unreasonable to assume that native hunters are aware of the reproductive parameters and limitations of their prey species. Native hunters following a conservation strategy might be expected to use their

³Many of the interviews were conducted with the assistance of Monica Gornikiewicz.

knowledge to minimize their impact on their prey (Ross, 1978). Hunters would identify those species most susceptible to uncontrolled harvesting and restrain from killing more than would be sustainable (e.g., Posey, 1982).

For the purpose of this paper, a "balanced" or sustainably harvest is defined as one that does not exceed the productivity of the prey and force the population into local depletion or extinction (see Robinson and Redford, 1991). Understanding how prey populations are sustainably harvested requires an understanding of how biological populations grow. One frequently used model of population dynamics is the logistic growth model (this discussion follows Richer, 1954; Caughley, 1977; Savidge and Ziesenis, 1980; Clark, 1990). The logistic equation (Eq. 1) defines the population growth rate as a density dependent function of population size, such that the increase in population size is inversely proportional to density.

$$dN/dt = r(1-N/K) \quad (1)$$

dN/dt = the rate at which the population is changing over time. When $dN/dt = 0$ the population is not growing. N = population size at any point in time. r = the intrinsic rate of increase, defined as the difference between the number of individuals born and the number of individuals that die. K = population size at carrying capacity.

This can be contrasted with a simple exponential model of growth, where populations grow exponentially without check. The logistic model

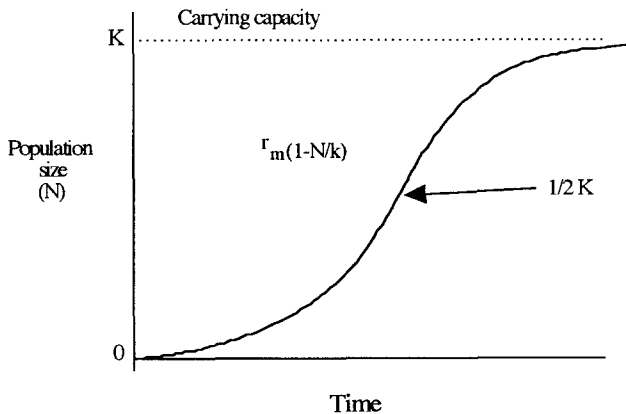


Fig. 2. Model of logistic growth. At low population densities, growth is rapid, exponential, and reaches a maximum at $1/2 K$. After this point, density related factors take effect and growth begins to slow to a point (carrying capacity) where the number of births equal the number of deaths, and growth is zero.

assumes animal populations increase exponentially until curtailed by factors related to intraspecific competition that limit increased growth (see. Fig. 2). These limiting factors could range from food, to nest sites, to increased disease due to overcrowding. At this point, called the carrying capacity (K), deaths equal births, $dN/dt = 0$ and the population size is stable. At this point, no *recruitment* into the population occurs. Figure 3 plots the relationship of growth rate, on the Y axis, to population size, on the X axis. Due to the density dependent effects, note that recruitment is highest at intermediate levels of population size.

Wildlife managers have used this model to examine the effects of harvesting on game (McCullough, 1984). For unharvested populations at carrying capacity, dN/dt is zero and any level of constant harvesting must bring the population size to some stable level below carrying capacity. For a harvest less than the maximum sustainable yield (see below), the population can be shown to have two points of equilibrium, X_1 and X_2 (Clark, 1990). If the prey population was initially greater than X_1 , a harvest below the maximum sustainable yield will push the prey population to point X_2 . This is the point where the harvest is compensated by recruitment. At that point the number of animals produced through reproduction equals the number killed by hunters. If the initial population was below X_1 , recruit-

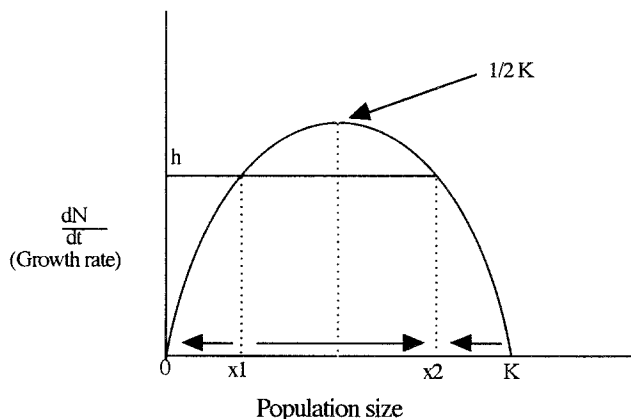


Fig. 3. Maximum sustainable yield model. Growth rate increases and decreases with population densities. At $1/2 K$, the rate is highest, and can sustain the maximum harvest. Harvests higher than this cannot be sustained and lead to extinction of the prey population.

ment cannot make up for the harvesting and the prey population will decline to zero.

At the point $.5K$ (half the carrying capacity), the growth rate of the population is highest because the density effects have not yet curtailed growth. It is at this point that the prey population can sustain the largest possible harvest (maximum sustainable yield—MSY). If the harvest is greater than the maximum sustainable yield, hunting will deplete the population to extinction no matter the initial size of the population.

Since the MSY depends on the prey population's growth rate, for the purposes of this paper the maximum intrinsic rate of increase (r_{\max}) will be used as a measure of a prey species' vulnerability to over-hunting and local extinction. r_{\max} is the maximum per capital instantaneous rate of increase for a species in an ideal environment not limited by factors such as resources or space (Caughley, 1977). Prey that reproduce faster can be harvested in greater numbers. Those that reproduce more slowly are at greater risk of depletion. r_{\max} is used here in place of r , because r can vary between populations of the same species in different habitats. r_{\max} is theoretically species-specific and thus is more useful for between-species comparison.

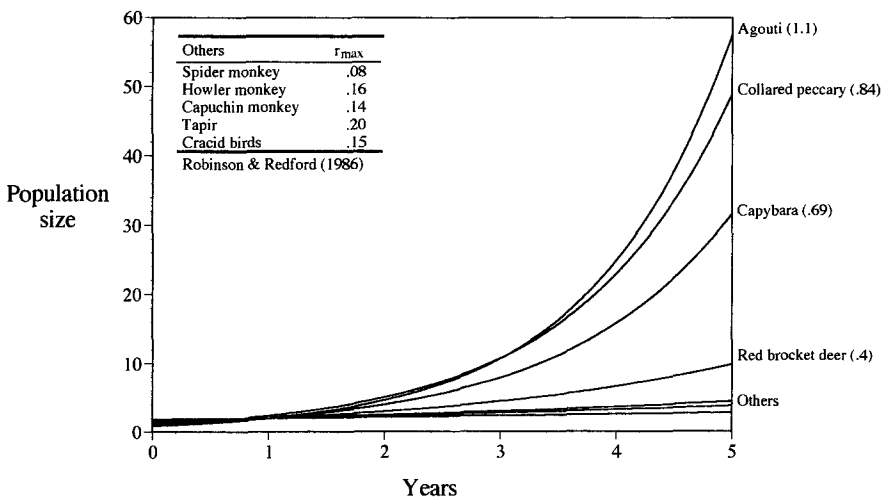


Fig. 4. Plot of the maximum intrinsic rate of increase for a number of the Piro prey species. Species identified as "other" include howler, spider, and capuchin monkeys, cracid birds, and tapir. This plot demonstrates the very large difference in reproductive potential, and vulnerability to local extinction of the various prey species among which the Piro have to choose.

Figure 4 graphically presents estimates of r_{\max} for a number of the Piro prey species. The r_{\max} values were calculated by Robinson and Redford (1986) using a formulation by Cole (1953) that incorporates age at first reproduction, age at last reproduction, and annual birth rate of female offspring. I estimated the r_{\max} for cracid game birds from information in Silva and Strahl (1991).⁴ It can be seen there is great variability in the growth rates of the Piro prey populations, and, thus, in the species' ability to withstand increasing levels of harvest. Collared peccaries, agoutis, and capybara have high r_{\max} ; such populations can reach high numbers quickly. In contrast, primates, tapir, and cracids have low r_{\max} and population growth is correspondingly much slower.

Reproductive rates vary according to phylogenetic relationships and diet, and relate allometrically to body size (Hennemann, 1983; Western, 1983; Robinson and Redford, 1986). Smaller animals tend to have higher reproductive rates than larger animals. Squirrels (~.5 kg) and agoutis (3–4 kg) have very high rates. Tapirs, on the other hand, which can weigh up to 200 kg, are slow reproducers; their r_{\max} approaches the absolute rate of the some of the primate species. Evidence suggests tapir populations quickly suffer depletion when subject to hunting (Fragoso, 1991).

Independent of body size, phylogenetic relationships predict growth rates too. Both before and after controlling for body size, the large primates have the lowest reproductive rates of all the Piro prey species. Robinson and Ramirez (1982) also conclude that the large primate species and particularly *Ateles*, because of its life history parameters, have a low recovery potential from population perturbations (see also Mittermeier and Cheney, 1987). In contrast, rodents, even the large (50 kg) species like capybara, have high reproductive rates.

The conclusions from this analysis on prey vulnerability are as follows. Collared peccary, agoutis, and capybara have characteristics that make them preferable prey species from a sustainability viewpoint. They are relatively large bodied, fast reproducers. Deer are large, though slower reproducing than capybara or collared peccary. I have shown that the primates are the most vulnerable species to overexploitation and local extinction. Tapir and cracid birds are also slow reproducing animals and relatively more vulnerable to overexploitation because of their slow reproductive rate (see Silva and Strahl, 1991).

Thus, if the Piro engage in any restraint to sustain the fauna around Diamante, it should be most apparent in the species identified as most

⁴According to Silva and Strahl (1991) cracids are characterized by a slow reproductive rate. They roughly estimate six years for replacement. This translates into an annual finite rate of increase of 1.16 or an intrinsic rate of increase of .15.

vulnerable to over-hunting. These are the large primate species (howler and spider monkeys), tapir, and the cracid game birds.

Foraging Theory

The goals of optimal foraging strategies, as they are usually constructed, contrast with the goals of conservation. Foraging theory assumes hunters have the proximate goal of short-term resource maximization, and no explicit or implicit statements about conserving the resource population are made.⁵ According to foraging theory, any regular intra- or interspecific variability in prey choice can be explained with reference to assumptions of short-term return maximization, without regard to the long-term sustainability of the harvest (Stephens and Krebs, 1986). From this point of view, selective harvests are the result of how profitably different prey types can be harvested, rather than how their harvest might effect the viability of the prey populations. While rate-maximizing hunting and sustained harvesting of prey are not necessarily mutually exclusive, any apparent conservation effect by optimal foraging is assumed to be only incidental to the goal of efficiency (Smith, 1983). In other words, any conservation effects are epiphenomenal (Hunn, 1982; Alvard, 1994).

The simple prey choice model used here generates strict predictions concerning which prey species hunters should pursue from the range of potential prey items encountered in order to maximize the harvest rate. Prey are ranked according to profitability. Profitability is calculated as the amount of energy harvested per unit time handling the prey, after encounter. Prey that are larger and/or more easily killed are the most profitable. Handling includes pursuit, kill, and processing, and is mutually exclusive of search time. A prey item is included the optimal diet⁶ if the expected return rate for pursuing that item upon encounter is higher than the expected average return rate for continued search for higher-ranked items. In other words, the forager asks himself upon encounter with a prey item:

⁵It is important to note that the time-span over which foraging theory assumes the return rate is maximized is over the "long term" (Stephens and Krebs, 1986). This is a rather ambiguous assumption, yet the time scale over which the return rate is maximized is very important when dealing with issues of conservation. Generations are often required for exploitive prey choice decisions to deplete prey populations (Rogers, 1991). From this perspective, the span over which most OFT analyses assume maximization is relatively *short term*, (over the course of one or several foraging bouts, Stephens and Krebs, 1986, p. 16). The assumption of selfish, short-term, rate-maximization made by foraging theory, and the assumption of long-term, common-good goals implicit in a conservation strategy, is the major contrast between the two hypotheses.

⁶The term "optimal diet" refers to the suite of prey types hunters are predicted by foraging theory to pursue during hunts, rather than the total Piro diet.

"Would I do better by handling this item, or should I spend the time searching for something better?" Formulated this way, the pursuit of a prey item not in the optimal diet results in a lower overall return rate than does continued search for more profitable prey; conversely, not pursuing a prey item that is in the optimal diet also leads to lower returns (Stephens and Krebs, 1986).

One prediction of this model is that hunters *always* take prey that are in the optimal diet, while those outside the optimal diet are *never* taken, regardless of their density in the environment (Stephens and Krebs, 1986). This is often referred to as the zero-one rule. Foragers that are observed sometimes to pursue a prey type, while at other times to ignore it, are said to have a *partial preference* for that prey (more on this below). This stringent prediction provides a contrast to what a prey choice rule derived from a conservation strategy might look like, since a conserving hunter might occasionally ignore prey vulnerable to local extinction. Evidence for conservation would be a partial preference for prey identified as vulnerable, yet which are calculated to be in the optimal diet.

Calculating the Piro Optimal Diet

The Piro optimal diet was calculated following Stephens and Krebs (1986). Three variables must be known for each prey type:

- h_i = handling time with an individual of type i after encounter
- e_i = average expected net energy gain after encounter with prey type i
- l_i = rate of encounter with prey type i

The profitability of prey type i is e_i/h_i . The prey are ranked according to their profitability, such that is $e_1/h_1 > e_2/h_2 \dots > e_n/h_n$. Beginning with the most profitable type (which is always included in the diet), prey are added to the diet, one by one, until a prey item is found that has a lower return rate upon encounter than could be obtained from searching for more profitable prey. That is, prey types are added to the diet until:

$$\frac{\sum_{i=1}^n \lambda_i e_i}{1 + \sum_{i=1}^n \lambda_i h_i} > \frac{e_{n+1}}{h_{n+1}} \quad (2)$$

Upon encounter with such a prey type, hunters could do better by ignoring it and all those less profitable, and continuing the search for types more profitable. This analysis predicts the prey items the Piro hunters

should pursue if they are hunting in a manner that maximizes return rates. This model also predicts which prey items are *not* in the optimal diet and never to be pursued on encounter. (2)

Table II contains the data used to determine the profitability for the sample of prey that were encountered during observed hunts (data are combined for both years in this analysis). Seven prey types are presented. Game birds are lumped to increase sample size. The analysis does not include prey for which I did not observe any kills because a measure of profitability cannot be calculated. Those excluded are important species such as capybara and tapir. Both were infrequently encountered during the deep forest, diurnal hunts I observed. The tapir is rare and mostly nocturnal, the capybara is riverine and nocturnal in hunted areas. Note that I could also not determine the profitability of prey the hunters did not pursue. As I will show, these animals include squirrels, tamarins, titi monkeys, squirrel monkeys, and numerous small birds. Predictions concerning these species will be discussed below.

Handling time includes both the time to pursue and the time to field process the prey.⁷ As mentioned, tracking prey is defined as search. For comparative purposes, I use the same estimates of calories per kilogram of prey as do Hill and Hawkes (1983); they assume 65% of the prey carcass is edible.

RESULTS: PIRO OPTIMAL PREY CHOICE

Figure 5 plots the major results presented in Table II. Plotted for each ranked prey item are: (1) the item's profitability, i.e., the mean return rate from pursuit, and (2) the mean return rate from continued search. This graph is comparable to those in Hill and Hawkes (1983), Kuchikura (1988), and Smith (1992).

Collared peccary is the most profitable prey type, followed by the agouti, the spider and howler monkeys, brocket deer, the game birds, and finally the capuchin monkey. These prey are either large packages of calories or types that can be taken with relatively short pursuits. The fact that the agouti is the second most profitable item demonstrates size is not always the most important factor determining a prey item's profitability. In this case, hunters dispatched the agoutis in short handling times. This will be discussed in more detail below.

⁷In the analysis I have included only processing activities in the forest in the handling values, because processing in the village is not at the expense of search time. This is a refinement that can be applied to central place foragers who do most of their handling at the central place.

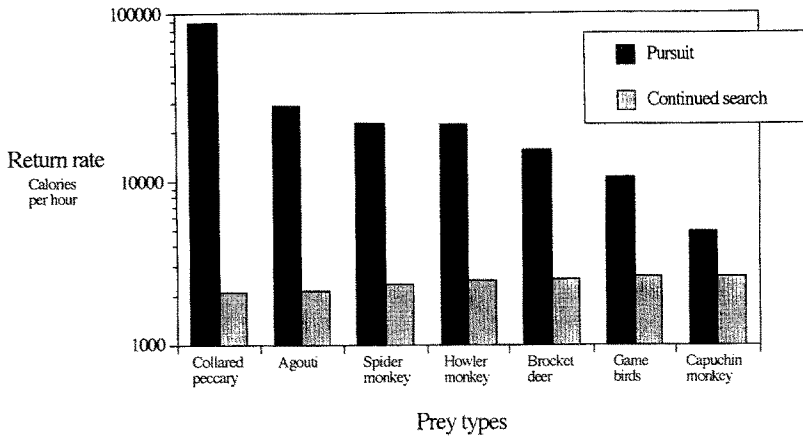


Fig. 5. Piro prey choice. At every prey encounter hunters have the option of pursuit or continued search. The bars represent the return rates from each decision. For each prey type presented in the graph, the optimal decision is pursuit (see text for details).

These results show that, for example, the choice to a Piro shotgun hunter when he has encountered a spider monkey is between pursuing the animal for an expected return of 22,916 calories per hour, or con-

Table II. Values Used to Calculate the Piro Optimal Diet^a

Prey	No. observed shotgun pursuits and kills	Pursuit and handling time (hr)	Harvest (kg)	Calories per kg	Calories harvested	Profitability	Rank	Hourly returns (this rank and above)
Collared peccary	31 (25)	11.5	519.4	1950	1,012,830	88,072	1	2103
Agouti	9 (2)	0.4	5.9	1950	11,505	28,762	2	2125
Spider monkey	8 (10)	4.7	82.5	1300	107,250	22,819	3	2325
Howler monkey	9 (10)	3.8	65.4	1300	85,020	22,383	4	2480
Deer	12 (1)	1.6	30.0	819	24,570	15,356	5	2522
Game birds	53 (25)	4.3	36.7	1240	45,508	10,583	6	2592
Capuchin monkey	20 (8)	7.5	28.6	1300	37,180	4,966	7	2627

tinuing to search for something more profitable for an expected return rate of 2,325 calories per hour. The two choices possible during a capuchin monkey encounter are closer in value. Pursuing a capuchin monkey returns an expected 4,933 calories per hour, while continued search returns only slightly less at 2,623 calories per hour. In both cases, the rate-maximizing choice, and the one predicted by the simple prey choice model, is pursuit.

Although the data do not exist for a determination, estimation suggests that rate-maximizing hunters should pursue capybara and tapir as well. If I conservatively estimate the mean handling time per kill for both prey types at 1 hour (the mean handling time per peccary kills is .47 hours), the profitability of tapir would be approximately 282,750 calories per hour of handling, and that of capybara is 61,425 calories per hour of handling. These values place both species well within the optimal diet.

The prey the Piro shotgun hunters did not pursue include squirrels, tamarins, titi monkeys, squirrel monkeys, and small birds (see below). Hunters told me that these prey types were too small to pursue with shotguns. To estimate a prediction, I used the handling parameters of similar prey for which data exist. A bird or squirrel weighing 500 grams at 1,200 cal/kg is a package of around 600 calories. The mean handling time for game bird kills was .17 hour. These estimates produce a profitability measure of 3,529 cal/hr. This is low, but within the range of shotgun hunters pursue. A squirrel monkey, on the other hand, which weighs around 800 grams is a package of about 1000 calories. If I use the mean pursuit time for capuchin monkeys of .93 hours, the profit measure of a squirrel monkey is 1,075 cal/hr; a hunter is predicted to ignore this animal.

It should be stressed that without information on the actual handling times these results are conjecture. It is reasonable to assume capybara and tapir should be included in the Piro optimal diet. Assuming the estimates are sound, these results predict it *may* also pay Piro shotgun hunters to pursue some of the small prey items that they ignore, especially if handling times are low. These results and their implications are discussed below.

Thus, the prediction of foraging theory is that the species included in Fig. 5 are in the optimal diet of the Piro hunters and should be pursued at every opportunity. These include collared peccary, agouti, spider and howler monkey, red brocket deer, game birds and capuchin monkeys. Also included are tapir and capybara. The smaller prey such as squirrels, small birds, and the small primates are very low ranked, and probably fall out of the optimal diet, although this depends on handling costs.

Table III. Encounters and Proportion Pursued for Observed Shotgun Hunts, 1988–1989 and 1990–1991

Prey	1990–1991 field season			1988–1989 field season			Combined sample
	No. encounters	No. pursuits	Pursued (%)	No. encounters	No. pursuits	Pursued (%)	Pursued (%)
Collared peccary	23	23	1.00	8	8	1.00	1.00
Spider monkey	5	5	1.00	3	3	1.00	1.00
Howler monkey	7	7	1.00	2	2	1.00	1.00
Coati	1	1	1.00	0	—	—	1.00
Duck	1	1	1.00	1	1	1.00	1.00
Paca	2	2	1.00	0	—	—	1.00
Ocelot	1	1	1.00	1	1	1.00	1.00
Capybara	1	1	1.00	1	1	1.00	1.00
Deer	11	10	0.91	3	2	0.66	0.86
Tapir	1	0	0.00	3	3	1.00	0.75
Capuchin monkey	13	7	0.54	17	13	0.76	0.67
Currassow	4	3	0.75	4	2	0.50	0.62
Macaw	17	5	0.29	14	7	0.50	0.38
Guan (<i>Aburria</i>)	8	2	0.25	16	7	0.44	0.37
White capuchin	1	1	1.00	2	0	0.00	0.33
Tinamous							
(<i>Tinamous</i>)	2	0	0.00	1	1	1.00	0.33
Spix's guan	65	13	0.20	23	8	0.35	0.24
Agouti	53	7	0.13	12	2	0.17	0.14
Tinamous							
(<i>Crypturellus</i>)	33	2	0.06	28	1	0.03	0.05
Trumpeter	20	1	0.05	1	0	0.00	0.05
Squirrel	58	0	0.00	19	0	0.00	0.00
Tamarin	26	0	0.00	11	0	0.00	0.00
Titi monkey	12	0	0.00	4	0	0.00	0.00
Squirrel monkey	10	0	0.00	12	0	0.00	0.00
Toucan	6	0	0.00	6	0	0.00	0.00
Turtle	5	0	0.00	4	0	0.00	0.00
Wood quail	3	0	0.00	3	0	0.00	0.00
Giant otter	2	0	0.00	2	0	0.00	0.00
Anteater	1	0	0.00	0	—	—	0.00
Armadillo	1	0	0.00	0	—	—	0.00
Bushdog	1	0	0.00	0	—	—	0.00
Hoatzin	1	0	0.00	1	0	0.00	0.00
Harpy eagle	1	0	0.00	0	—	—	0.00
Night monkey	1	0	0.00	0	—	—	0.00
Nutria	1	0	0.00	0	—	—	0.00
Puma	1	0	0.00	1	0	0.00	0.00
Sloth	1	0	0.00	1	0	0.00	0.00
Tayra	1	0	0.00	0	—	—	0.00

Table IV. Encounters and Proportion Pursued for Unobserved Bow and Shotgun Hunts, 1990–1991

Prey	1990–1991 unobserved shotgun hunts			1990–1991 unobserved bow hunts		
	No. encounters	No. pursuits	Pursued (%)	No. encounters	No. pursuits	(%) Pursued
Deer	15	15	1.00	8	8	1.00
Duck	1	1	1.00	0	—	—
Spider monkey	7	7	1.00	0	—	—
Collared peccary	25	23	0.92	14	14	1.00
Howler monkey	7	6	0.86	2	2	1.00
Tapir	5	4	0.80	2	2	1.00
Capuchin monkey	13	4	0.29	4	4	1.00
Titi monkey	4	1	0.25	11	11	1.00
Macaw	11	2	0.18	4	3	0.75
Tinamous (<i>Crypturellus</i>)	15	2	0.13	11	10	0.91
Trumpeter	8	1	0.12	2	2	1.00
Squirrel monkey	11	1	0.09	17	15	0.88
Guan (<i>Aburria</i>)	13	1	0.08	12	11	0.92
Agouti	27	2	0.07	19	19	1.00
Spix's Guan	18	1	0.05	11	11	1.00
Curassow (<i>Minu</i>)	1	0	0.00	8	8	1.00
Anteater	2	0	0.00	1	1	1.00
Armadillo	1	0	0.00	5	4	0.80
Giant Otter	1	0	0.00	0	—	—
Night Monkey	1	0	0.00	3	3	1.00
Ocelot	1	0	0.00	0	—	—
Tinamous (<i>Tinamous</i>)	1	0	0.00	8	8	1.00
Wood quail	1	0	0.00	0	—	—
Squirrel	17	0	0.00	18	18	1.00
Tamarin	16	0	0.00	2	1	0.50
Toucan	5	0	0.00	1	1	1.00
Turtle	7	0	0.00	18	0	0.00
Bushdog	0	—	—	0	—	—
Capybara	0	—	—	6	6	1.00
Coati	0	—	—	0	—	—
Harpy Eagle	0	—	—	0	—	—
Hoatzin	0	—	—	2	0	0.00
Nutria	0	—	—	0	—	—
Paca	0	—	—	1	1	1.00
Puma	0	—	—	0	—	—
Sloth	0	—	—	0	—	—
Tayra	0	—	—	1	0	0.00

RESULTS: ACTUAL PIRO PREY CHOICE

Pursuit decisions during hunts are the most appropriate level of analysis to determine if Piro hunters choose prey according to foraging theory

predictions or show restraint as suggested by the conservation strategy. Table III presents data on encounters and pursuits of shotgun hunters from the observed hunt sample. Table IV present data on encounters and pursuits during unobserved shotgun and bow hunts. The number of encounters and pursuits are recorded for each species. In addition, the percentage of encounters that hunters pursued has been calculated.

The data show that the prey fall into three categories: (1) those that were always or almost always pursued, (2) those that were never pursued, and, (3) those that were inconsistently pursued.

The commonly encountered prey types that were always or almost always pursued by Piro shotgun hunters were the large species. Collared peccaries were pursued at every encounter except for two cases during unobserved hunts when shells were not available. Spider monkeys, howler monkeys, capybara, deer, and tapir were also pursued at nearly every encounter. Occasionally one of these types was not pursued; this will be discussed below.

There are a number of prey types that Piro shotgun hunters never pursue. Some of these animals are large and may have yielded profitable returns. These are rarely encountered species, although they not necessarily rare in the forest (Alvard, 1993). These include the anteater, puma, bush-dog, caiman, sloth, tayra, and otters. Some of these animals are taboo (e.g., the caiman). Others, the Piro simply do not eat (e.g., sloth), although other human groups nearby do. Discussion with hunters, and limited data from unobserved hunts, indicate these prey types are not pursued with bow either, suggesting the decision to ignore these animals does not relate to technology. Since this is a potentially conservative behavior, I will discuss below why the Piro may ignore these animals.

Tables III and IV also present data on the small types that may fall into the optimal diet yet Piro shotgun hunters also never pursued. These include squirrels, squirrel monkeys, tamarins, titi monkeys, and small birds. These species are encountered quite frequently (Alvard, 1993), and in contrast to the other larger, rare prey types that are never pursued, data from unobserved hunts show that bow hunters usually pursue these animals (see Table IV), indicating a factor related to hunting technology may be important.

More interesting for the question at hand are the prey that hunters pursue *inconsistently*. These species are lower ranked types, including agoutis, the game birds, and capuchin monkeys. While agoutis are not among the species identified as more vulnerable to over hunting, the cracids and capuchins are candidates for local depletion. This presents the possibility that the Piro hunters ignore harvesting opportunities to conserve these species.

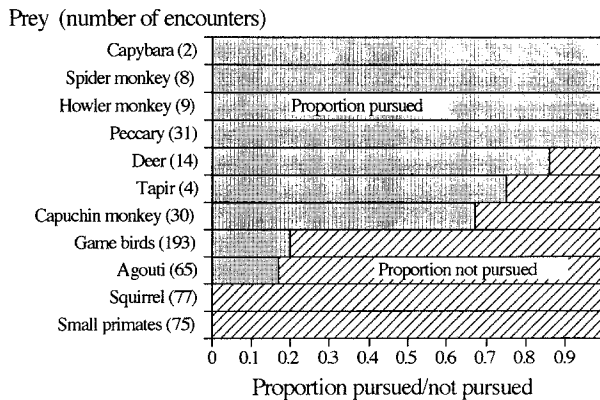


Fig. 6. Proportion of encounters pursued by shotgun hunters. The number of encounters for each prey type is indicated in parentheses. Note that capybara, collared peccary, and both species of large primates were always pursued. A small proportion of deer and tapir were not pursued. Capuchin monkeys, game birds, and agoutis were not regularly pursued. Small primates and squirrels were never pursued. Details in text.

DISCUSSION

The prey items that are always pursued by Piro shotgun hunters closely match those predicted by foraging theory. These are large, high ranked animals in the optimal diet. All but two collared peccaries, the most important species numerically as well in terms of weight, were always pursued when encountered during hunts. Howler and spider monkeys, the large primates, and the prey species most vulnerable to extinction, were always pursued. Deer, tapir, and capybara were almost always pursued when encountered. This result provides general support for the foraging model. The observation that no restraint was shown killing the large primate species is the strongest evidence contrary to the conservation hypothesis.

While the status of the smaller prey (small primates, squirrels, small birds) is ambiguous as to whether they fall in or out of the optimal diet, I argue that their exclusion by shotgun hunters is consistent with the foraging hypothesis. Their low ranking reflects a general unprofitability and the discussion that follows will show that inherent costs in shotgun hunting make these small species even less profitable.

Partial Preferences

Among some of the other lower ranked prey there is considerable deviation from the all or nothing pursuit decision predicted by the simple prey choice model. As mentioned above, the zero-one rule is one of the basic predictions of the simple prey choice model. According to this rule, albeit under the rather rigid assumptions of the model, prey types should either *always* be pursued, or *never* pursued (Stephens and Krebs, 1986). The Piro break this rule when they ignore a particular species on some occasions, while pursuing them on others. This is referred to as a partial preference (Krebs and McCleery, 1984).

Figure 6 graphically presents pursuit data for the combined observed hunt sample, and shows shotgun hunters have a partial preference for a number of species. During observed hunts, 14% of the agoutis encountered were pursued, only 24% of the spix's guans were pursued, and 66% of the capuchin monkeys were pursued. Note that hunters even occasionally did not pursue large, high ranked animals when the opportunity presented itself. These behaviors present the possibility that the Piro are conserving these species by restraining their harvesting. A conservation strategy predicts that the species hunters might occasionally avoid would be those most vulnerable to local extinction (see above), i.e., species whose reproductive rates are low. It is also possible that conserving hunters are ignoring certain age and sex types within species (Alvard, 1993). Selective intraspecific prey choice will be discussed in a more detail in a subsequent paper.

I hesitate, however, to invoke conservation as a reason for these partial preferences for two reasons. First, the Piro partial preferences are not consistent with the predictions of the conservation strategy. Some of the species for which the Piro have partial preferences are not particularly vulnerable to local extinction. Agoutis, for example, are exceedingly fast breeders. Also, as noted above, the hunters do not have partial preferences for the species where it is most expected, the vulnerable large primates.

Second, while the pattern of Piro partial preferences is not satisfactorily explained by the conservation hypothesis, there are a number of more complex models within the scope of foraging theory that *can* explain them. I will first examine attack limitations as an explanation for the partial preferences, then discuss how encounter-variability may play a role. To examine these ideas I will use as examples the game birds and agoutis, and then argue the same explanations account for the other partial preferences as well.

Attack Limitations

The appearance of partial preferences can occur when the factors that determine the profitability of a prey type vary with location or time (Krebs and McCleery, 1984; McNamara and Houston, 1987). Although the decision to pursue an item is independent of its *own* encounter rate, inclusion in the diet is affected by the density of higher ranked items in the environment. Foraging theory predicts that if higher ranked prey become more common in the habitat, diet constriction occurs and lower ranked items drop out of the diet. As encounter rates with higher ranked prey decrease, lower ranked items should be included in the diet (Pyke *et al.*, 1977).

An example of this effect with human hunters is developed by Hames and Vickers (1982), who examined variability in prey choice among Yanomamo, Yekwana, and Siona-Secoya hunters of Amazonia. Hames and Vickers noted that in areas where depletion due to hunting has occurred the density of higher ranked items increased with distance from village. In this situation, foraging theory predicts diet breadth should narrow and lower ranked items should drop out of the diet as hunters move away from the village. As the rate of encounters with higher ranked prey declines, as happens near villages, the diet should broaden to include types excluded further out. Hames and Vickers (1982) showed that among the Yanomamo and Yekwana, hunters killed lower ranked game more frequently closer to the villages than further away. Hunters took higher ranked game more often in the further zones. If lower ranked items were present in the further zones (very likely) this implies that hunters did not pursue lower ranked game items when encountered further away, but did when closer to the village. This is a partial preference, neatly explained by optimal foraging.

While this partial preference effect is definitely related to depletion the situation may be more complex than Hames and Vickers' interpretation, especially when hunters are "attack-limited" as are shotgun hunters. Most optimal foraging models implicitly assume that a predator can attack as many times as it chooses (Stephens and Krebs, 1986). Attack-limited refers to the constraint faced by foragers who are restricted in the number of pursuits possible during a foraging bout (Alvard, 1993). Such foragers hunt with the constraint that an attack at time A, precludes an attack later on a different animal at time B. In the case of shotguns, attacks are limited to the number of shells in the possession of the hunter. The noise made by shotgun blasts may also preclude further encounters by scaring game away from the hunting area. Bow hunters who carry few arrows that are easily lost may suffer from this problem as well.

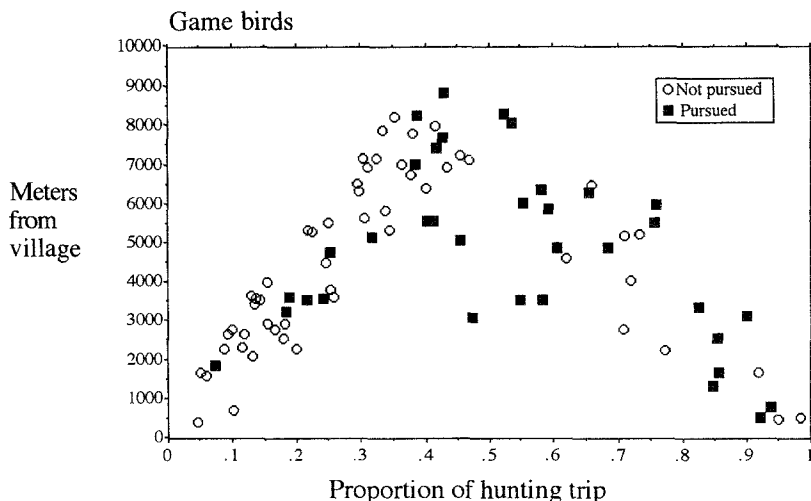


Fig. 7. The timing of game-bird pursuits. Hunters are significantly more likely to pursue game birds as hunts progress (Chi-square = 20.80, $p = .0001$). Each encounter was identified at a point in time, relative to the total length of the hunt. If the hunt was 7 hr long, and an agouti was encountered after 5 hr into the hunt, the proportion of the hunt that elapsed was .71. Points rise as hunters move away from the village and fall as they reach a turn around point and head back.

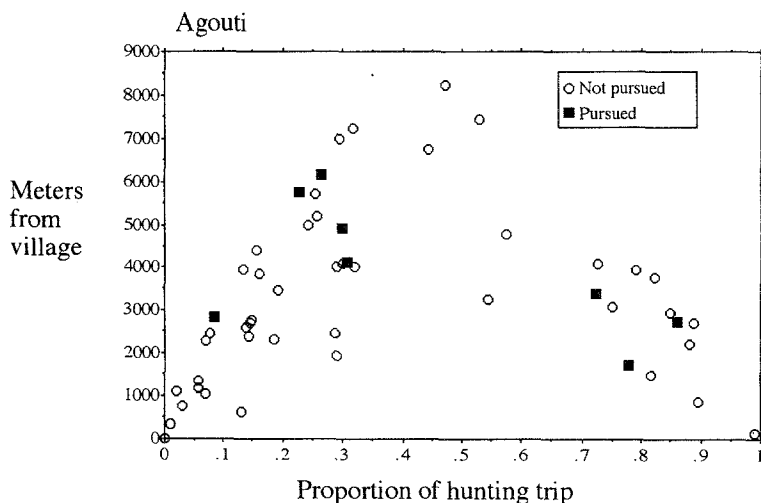


Fig. 8. The timing of agouti pursuits. Unlike game bird partial preferences, hunters are not more likely to pursue agoutis on the return portion of their trips (Chi-square = 1.3, $p = .253$).

It was apparent during hunts that Piro shotgun hunters made pursuit decisions by taking into account attack limitations and the opportunity costs involved in shooting smaller sized animals. On a number of occasions, hunt-

ers expressed to me, upon encountering a game bird early in a hunt, that they would pass it up now, but would kill the bird on the way back if they did not kill anything else. The probability of encountering a high ranked animal during the remaining portion of the hunt is greatest in the hunt's initial stages, and decreases as the hunt progresses. This is simply because, assuming some limit to the length of the hunt, the time remaining to encounter prey decreases. If a hunter has a limited number of shells, shooting a lower ranked item early in the hunt, even if it is in the optimal diet as calculated by the simple model, may not maximize the hunt's return rate. As a hunt draws to a close, and the likelihood of encountering a large prey type declines, a point is reached when hunters do better by killing a small item if one is encountered, than waiting for a larger one.⁸

Attack-limited hunting, in combination with variable encounter rates due to depletion effects, predicts partial preferences for some lower ranked prey. Game birds were the most frequently ignored prey in the Piro optimal diet and are among the prey types identified as vulnerable to over hunting. Data on when during the hunts hunters pursued these sometimes-pursued prey provide support for the idea that attack limitations explain hunters' partial preferences. As predicted by the attack-limited model, A Chi-square test shows that game birds are significantly more likely to be pursued after half the hunt is over (on the way back) than in the first half of the hunt (Chi-square = 2.18, $p = .0001$). This result is graphically presented in Fig. 7, and supports the idea that hunters are holding off their pursuits of birds on the hopes of using their shells to kill larger animals.

Encounter Variability

The pattern evident for game birds is not the same for agoutis or capuchin monkeys. Pursuits of these types were equally likely to occur in the first half of the hunt as the last half (Chi-square = 1.3, $p = .253$; see Fig. 8; Alvard 1993). The different pattern for agoutis may be related to reasons offered by Hill *et al.* (1987) and Smith (1991, p. 205). They suggest that context-specific variation plays a role in patterning preferences. As mentioned above, the profitability of a prey item is the return upon encounter, i.e., the caloric return per unit handling time. In reality, what is *measured* is the return upon *pursuit*. Observers can only measure what hunters pursue. If the hunter chooses not to pursue, that encounter contributes

⁸This model assumes that the return rate *during the hunt* is to be maximized. Also implicit in the argument is that some minimal amount of resource is desired. Without this last assumption, a hunter might as well save his shell for the next day's hunt. For more details of this model see Alvard (1993).

no information to the measure of profitability. The data used to measure the profitability of a prey type are biased toward encounters that were favorable enough to invite pursuit. There exists much variability in the nature of encounters not considered in the measure of profitability.

Agoutis are a good example. Agoutis are often encountered when they give an alarm bark and flee. Such encounters are never pursued by shotgun hunters. Most of the agoutis that were killed were in situations where the agouti was observed by the hunter but the agouti was unaware the hunter was near. The latter type of encounter provides high returns because of low handling times. While there are no confirming data, pursuing a fleeing agouti through the forest would likely result only in frustration. These two types of agouti encounters explain why agoutis are the second most profitable prey item, yet were not always pursued. The partial pursuits of agoutis are really a product of the context of encounter. An encounter with an agouti that has seen the hunter first is different from an encounter with one that has not seen the hunter first.

I argue that a combination of attack limitations and variable encounter explains most of the situations when capuchin monkeys, tapir, and deer were not pursued, though there are a number of exceptions. Two peccaries and three capuchin monkeys were not pursued in the unobserved sample because the hunters did not have shells. One deer was ignored because of adherence to a taboo against killing deer. Deer were thought by some Piro to be the spirits of the deceased. While it is obvious this taboo was not followed by most hunters, one man ignored an opportunity to kill a deer for this reason.

For most of the other larger species that were never pursued, like anteaters, bushdog, puma, and sloth, hunters had less idealistic explanations for avoidance; they displayed revulsion and said the meat was simply not good. People communicated this in a manner not unlike a North American might discuss eating horse meat.

This issue is clearly not one of conservation however, because the Piro almost never kill these animals. This is a point brought up by Bernard Nietschmann (1978, p. 24) in a reply to Eric Ross's (1978) article on food taboos in Amazonia. Ross argues Achuara Indians of Peru taboo prey species susceptible to overexploitation. But "... why conserve what is not used?" argued Nietschmann (1978, p. 24). Tabooing the killing of useful animals is a reasonable argument; an example is the Hindu ban on killing cows that are indispensable as draft animals (Harris, 1977). Explanations of why Piro hunters do not pursue sloths (for example), however, must look beyond sloth conservation.

As noted above, one incongruity is that a number of these small prey items *may* be profitable enough that shotgun hunters should pursue them

according to the prey choice model. In other words, the Piro shotgun hunters have a more constricted diet than may be predicted by the prey choice model. A more parsimonious explanation is that the attack-limited nature of shotgun hunting, mentioned above, and the cost of shotgun shells makes pursuing them too costly. If shotgun shells were as abundant and easily obtained as arrows, the small prey types would be more often pursued by shotguns.

Bow Hunts

Many species that were consistently ignored by shotgun hunters were consistently pursued when the same men hunted with bows. Since I observed no bow hunts, however, the optimal bow diet could not be calculated. Work by Hill and Hawkes (1983) with the bow-hunting Aché is informative concerning the effects of hunting technology on prey choice. They show that foraging theory predicts a broadening of the diet with a change to the less efficient bow technology. That is, bow hunters are predicted to include less profitable items ignored by shotgun hunters. This is because shotguns are much more efficient at killing in general, including the large, more profitable prey (see also Hames, 1979; Alvard and Kaplan, 1991). With greater efficiency, shotgun hunters do worse by pursuing small game, and better by focusing on the larger prey. Bow hunters, on the other hand, can increase their over all return rates by pursuing smaller game that the shotgun hunters ignore.

The prey choice of Piro bow hunters reported from unobserved bow hunts supports this prediction (see Table IV). Bow hunters pursued many of the small types shotgun hunters either ignored or inconsistently pursued. For example, squirrels, and many of the small primates, such as squirrel monkeys, tamarins, night monkeys and titi monkeys, were never pursued by shotgun hunters, but almost always pursued when bows were the weapon. This supports the conclusion that it is the costs and benefits of pursuing alternative prey that determine the decision to pursue or not, rather than a concern for the sustainability of the harvest.

CONCLUSION

The contributions of this quantitative study, and the others that will follow, are twofold. The first lies with the development and use of an operational definition of conservation that allows empirical tests. The definition of conservation presented above, which emphasizes short-term costs

rather than sustainable harvests, avoids the problem of confusing epiphenomenal conservation with genuine conservation. The second contribution is that with a robust definition of conservation, a number of tests, in addition to the one offered here, are possible.

While the results of the test presented here do not support the hypothesis that the Piro choose between alternative prey types in a manner consistent with a strategy designed to conserve their faunal resources, neither does it completely reject it. A comprehensive test for conservation would look for a variety of tactics where short-term costs are paid for longer-term benefits. For example, selective intra-specific prey choice is also available to hunters as a method for managing prey populations. Skewing a harvest toward individuals of lower reproductive value such as younger, older, and male individuals can increase the maximum sustainable yield (MacArthur, 1960; Caughley, 1977; Hayne and Gwynn, 1977).

It is also possible that the Piro hunters might spend less time hunting than would be in their short-term best interest in order to minimize the impact of the prey. Hames (1987) examined this question with cross-cultural comparative data and found a pattern that did not support a conservation hypothesis. Assuming that return rates were indicative of prey abundance, Hames found that hunters spend more time hunting when prey are depleted, and less when returns are high. This is just the reverse from what would be predicted if the hunters were conservationists. The results of such tests with the Piro data are forthcoming (see also Alvard, 1993).

A possible criticism of this study is that the Piro's non-conservationist behavior is due to deterioration of a traditional cultural system that perhaps was more conservation oriented in the past. It is conceded that the Piro could have behaved differently in the past, although this is very difficult to determine. One could argue that since resource acquisition is such an important aspect of survival, strategies like conservation might be very conservative and resistant to the influences of acculturation. This is perhaps naive. If conservation was common in the Piro past, its deterioration might be indicative of how vulnerable such an adaptation is to invasion by other strategies. This is to say, conservation may develop in small isolated populations, but because of the long-term payoff schedule inherent in such a strategy, it may be very vulnerable to replacement by ideas that offer shorter-term benefits.

In spite of evidence against the conservation hypothesis for the Piro case, it must be stressed that Diamante is just one community with a particular history and set of circumstances. It would not be prudent to generalize at this time and say all native hunting people choose their prey in

the same ways as Diamante hunters, or to say that all indigenous people over-exploit their faunal resources. Most Amazonian groups that have been studied by modern ethnographers live at low densities and in dispersed settlements (Gross, 1975). That these groups apparently live within the limits of their environment is evidence that some sort of apparent equilibrium has been achieved. However, as discussed above, such a circumstance does not rate the hunters the label of conservationists. Hunters can hunt exactly according to the assumptions of foraging theory but still harvest less than the maximum sustainable. Additional comparative work must be done to determine what causes some groups to overhunt and others not. It is anticipated that research of this sort will provide support for the idea that the appearance of balance between traditional native groups and their environment has more to do with low human population densities, lack of markets, and limited technology than it does with any natural harmonious relationship with nature (Alvard, 1993).

As these factors related to consumer demand change and the system is perturbed, the "balance" can easily tip toward overexploitation. The native populations of Amazonia are not the cause of the ecological crisis that grips the region today, but they probably do not represent the only solutions either. Native populations are expected to desire the same material benefits that other, more developed peoples enjoy, such as adequate nutrition, shelter, health care, and education. It is also expected that they will to exploit the resources that are available to them to achieve these ends, unless alternative means are obtainable. Recognizing that the native populations of Amazonia are not likely to behave as altruists is the first step to incorporating them into a general solution.

ACKNOWLEDGEMENTS

I am grateful to Hillard Kaplan, Jane Lancaster, Jeff Long, and Kent Redford for assistance and guidance. Many thanks to Teslin Phillips, Kate Kopischke, and Monica Gornikiewicz who assisted with data collection. Special thanks to Sharon Gursky for encouragement, support, and critical comment. To the Piro of Diamante, appreciation for allowing me into to their lives and along on their hunts. Much gratitude goes to Alejandro Smith, and Estefan Carpio and family for assistance in the field. This research was supported by the Charles Lindbergh Foundation, the L.S.B. Leakey Foundation, the Tinker Inter-American Research Foundation, the University of New Mexico, and the National Science Foundation (Grant BNS-8717886 to Hillard Kaplan).

REFERENCES

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behavior* 49: 227-267.
- Alvard, M. (1993). Testing the Ecologically Noble Savage Hypothesis: Conservation and Subsistence Hunting by the Piro of Amazonian Peru. Ph.D. Dissertation, University of New Mexico, Albuquerque.
- Alvard, M. (in press). Conservation by native peoples? Prey choice in a depleted area. *Human Nature*.
- Alvard, M., and Kaplan, H. (1991). Procurement technology and prey mortality among indigenous neotropical hunters. In Stiner, M. (ed.), *Human Predators and Prey Mortality*. Westview Press, Boulder, pp. 79-104.
- Berlin, O., and Berlin, E. (1977). *Etnobiología, Subsistencia y Nutrición en una Sociedad de la Selva Tropical: Los Aguaruna*. University of California Press, Berkeley.
- Bodley, J. (1976). *Anthropology and Contemporary Human Problems*. Benjamin Cummings Publishing, Menlo Park, California.
- Bodley, J. (1990). *Victims of Progress* (3rd Ed.). Mayfield Publishing, Mountainview, CA.
- Borgerhoff-Mulder, M., and Caro, T. (1985). The use of quantitative observational techniques in anthropology. *Current Anthropology* 26: 323-335.
- Bunyard, P. (1989). Guardians of the Amazon. *New Scientist* 35: 38-41.
- Camino, A. (1977). Trueque, correrías e intercambios entre los Quechuas Andinos y los Piro y Machiguenga de la montaña Peruana. *Amazonía Peruana* 1: 1-27.
- Caughley, G. (1977). *Analysis of Vertebrate Populations*. John Wiley & Sons, London.
- Clark, C. (1990). *Mathematical Bioeconomics: The Optimal Management of Renewable Resources*. John-Wiley & Sons, New York.
- Clay, J. (1988). *Indigenous Peoples and Tropical Forests: Models of Land Use and Management from Latin America*. Cultural Survival, Cambridge.
- Cole, L. (1954). The population consequences of life history phenomena. *Quarterly Review of Biology* 29: 103-137.
- Diamond, J. (1986). The golden age that never was. *Discover* 9: 70-79.
- Fragoso, J. (1991). The effect of hunting on tapirs in Belize. In *Neotropical Wildlife Use and Conservation*. Robinson, J., and Redford, K. (eds.), Chicago University, Chicago, pp. 154-162.
- Gentry, A. (1990). *Four Neotropical Forests*. Yale University Press, New Haven.
- Gross, D. (1975). Protein capture and cultural development in the Amazon. *American Anthropologist* 77: 526-549.
- Hames, R. (1979). A comparison of the efficiencies of the shotgun and the bow in neotropical forest hunting. *Human Ecology* 7: 219-252.
- Hames, R. (1987). Game conservation or efficient hunting? In McCay, B., and Acheson, J. (eds.), *The Question of the Commons*. University of Arizona Press, Tucson, pp. 97-102.
- Hames, P. (1991). Wildlife Conservation in tribal societies. In Oldfield, M., and Alconn, J. (eds.), *Biodiversity; Culture, Conservation and Ecodevelopment*. Westview Press, Boulder, CO, pp. 172-199.
- Hames, R., and Vickers, W. (1982). Optimal diet breadth theory as a model to explain variability in Amazonian hunting. *American Ethnologist* 9: 357-378.
- Hardin, G. (1968). The tragedy of the commons. *Science* 162: 1243-1248.
- Harris, M. (1977). *Cannibals and Kings*. Random House, New York.
- Hayne, D., and Gwynn, J. (1977). Percentage does in total kill as a harvest strategy. *Proceedings of the Joint Northwest-Southwest Deer Study Group Meeting*, pp. 117-127.
- Heinen, J., and Low, B. (1992). Human Behavioral Ecology and environmental conservation. *Environmental Conservation* 19: 105-116.
- Hennemann, W. (1983). Relationship among body mass, metabolic rate and the intrinsic rate of natural increase in mammals. *Oecologia* 56: 104-108.
- Hill, K., and Hawkes, K. (1983). Neotropical Hunting among the Ache of Eastern Paraguay. In Hames, R., and Vickers, W. (eds.), *Adaptive Responses of Native Amazonians*. Academic Press, New York, pp. 139-188.

- Hill, K., Kaplan, H., Hawkes, K., and Hurtado, A. (1987). Foraging decisions among Ache hunter-gatherers. New data and implications for optimal foraging models. *Ethnology and Sociobiology* 8: 1-36.
- Holdrige, L. (1967). *Life Zone Ecology*. Tropical Science Center, San José, Costa Rica.
- Hughes, J. (1983). *American Indian Ecology*. Texas Western Press, El Paso.
- Hunn, E. (1982). Mobility as a factor limiting resource use in the Columbia Plateau of North America. In Williams, N., and Hunn, E. (eds.), *Resource Managers: North American and Australian Hunter-Gatherers*. Westview Press, Boulder, pp. 17-43.
- Kaplan, H., and Hill, K. (1992). The evolutionary ecology of food acquisition. In Smith, E., and Winterhalder, B. (eds.), *Evolutionary Ecology and Human behavior*. New York, Aldine de Gruyter, pp. 167-202.
- Kay, J. (1990). *Yellowstone's Northern Elk Herd: A Critical Evaluation of the "Natural Regulation" Paradigm*. Ph.D. dissertation, Utah State University, Logan.
- Krebs, J., and McCleery, R. (1984). Optimization in behavioral ecology. In Krebs, J., and Davies, N. (eds.), *Behavioral Ecology: An Evolutionary Approach*. Sinauer Associates, pp. 91-121.
- Kuchikura, Y. (1988). Efficiency and focus of blowgun hunting among Semaq Beri hunter-gatherers of peninsular Malaysia. *Human Ecology* 16: 271-305.
- Lewontin, R. (1970). The units of selection. *Annual Review of Ecology and Systematics* 1: 1-18.
- MacArthur, R. (1960). On the relation between reproductive value and optimal predation. *Proceedings of the National Academy of Science* 46: 143-145.
- McCay, B., and Acheson, J. (eds.) (1987). *The Question of the Commons*. University of Arizona Press, Tucson.
- McCulloch, D. (1984). Lessons from the George Reserve, Michigan. In Halls, L. (eds.), *White Tailed Deer: Ecology and Management*. Stackpole Books, Harrisburg, PA, pp. 211-242.
- McDonald, D. (1977). Food taboos: A primitive environmental protection agency: *Anthropos* 72: 734-748.
- McNamara, J., and Houston, A. (1987). Partial preferences and foraging. *Animal Behavior* 35: 1084-1099.
- Meggors, B. (1971). *Amazonia: Man and Culture in a Counterfeit Paradise*. Aldine-Atherton, Chicago.
- Mittermeier, R., and Cheney, D. (1987). Conservation of primates and their habitats. In Smuts, B., Cheney, D., Seyfarth, R., Wrangham, R., and Struhsaker, T. (eds.), *Primate Societies*. Chicago University Press, Chicago, pp. 477-490.
- Nietschmann, B. (1978). Comments on Ross. *Current Anthropology* 19: 24-25.
- Posey, D. (1982). Indigenous ecological knowledge and development of the Amazon. In Moran, E. (ed.), *The Dilemma of Amazonian Development*. University of Colorado, Boulder, pp. 225-257.
- Posey, D. (1985). Native and indigenous guidelines for new Amazonian development strategies: Understanding biodiversity through ethnology. In Hemming, J. (ed.), *Change in the Amazon*. Manchester University Press, Manchester, pp. 156-181.
- Pyke, G., Pulliam, H., and Charnov, E. (1977). Optimal foraging: A selective review of theory and tests. *Quarterly Review of Biology* 52: 137-154.
- Redford, K. (1991). The ecologically noble savage. *Orion* 9: 24-29.
- Ricker, W. (1954). Stock and recruitment. *Journal of the Fish Research Board of Canada* 11: 559-623.
- Robinson, J., and Redford, K. (1986). Intrinsic rate of natural increase in Neotropical forest mammals: Relationship to phylogeny and diet. *Oecologia* 68: 516-520.
- Robinson, J., and Ramirez, J. (1982). Conservation biology of neotropical primates. *Special Publication of the Pymatuning Laboratory of Ecology* 6: 329-344.
- Robinson, J., and Redford, K. (1991). Sustainable harvest of neotropical wildlife. In Robinson, J., and Redford, K. (eds.), *Neotropical Wildlife Use and Conservation*. Edited by University of Chicago, Chicago, pp. 415-429.
- Rogers, A. (1991). Conserving resources for children. *Human Nature* 2: 73-82.
- Ross, E. (1978). Food taboos, diet, and hunting strategy: The adaptation to animals in Amazon cultural ecology. *Current Anthropology* 19: 1-36.

- Savidge, I., and Ziesenis, J. (1980). Sustained yield management. In Schmnitz, S. (ed.), *Wildlife Management Techniques Manual*. The Wildlife Society, Washington, D.C., pp. 405-410.
- Silva, J., and Strahl, S. (1991). Human impact on populations of chachalacas, guans, and curassows (Galliformes: Cracidae) in Venezuela. In Robinson, J., and Redford, K. (eds.), *Neotropical Wildlife Use and Conservation*. Chicago University Press, Chicago, pp. 37-52.
- Simms, S. (1992). Wilderness as human landscape. In Zeveloff, S., Vause, L., and McVaugh, W. (eds.), *Wilderness Tapestry: An Eclectic Approach to Preservation*. University of Nevada Press, Reno, Nevada, pp. 183-201.
- Smith, E. (1983). Anthropological applications of optimal foraging theory: A critical theory. *Current Anthropology* 24: 625-651.
- Smith, E. (1991). *Inujjamiut Foraging Strategies: Evolutionary Ecology of an Arctic Hunting Economy*. Aldine, New York.
- Smith, E. (1992). Human behavioral ecology. *Evolutionary Anthropology* 1: 20-25.
- Speck, F. (1939). Aboriginal conservators. *Bird Lore* 40: 258-261.
- Stephens, D., and Krebs, J. (1986). *Foraging Theory*. Princeton University Press, Princeton.
- Terborgh, J. (1983). *Five New World Primates*. Princeton University Press, Princeton.
- Terborgh, J., Fitzpatrick, J., and Emmons, L. (1984). An annotated list of the birds and mammals of Cocha Cashu Biological Station. *Fieldiana* 21: 1-29.
- Western, D. (1983). Production, reproduction and size in mammals. *Oecologia* 59: 269-271.
- Williams, G. (1966). *Adaptation and Natural Selection*. Princeton University Press, Princeton.
- Wynne-Edwards, V. (1962). *Animal Dispersion in Relation to Social Behavior*. Hafner, New York.
- Yost, J., and Kelly, P. (1983). Shotguns, blowguns, and spears: The analysis of technological efficiency. In Hames, R., and Vickers, W. (eds.), *Adaptive Responses of Native Amazonians*. Academic Press, New York, pp. 189-224.